Title: Fine-scale behavioural adjustments of prey on a continuum of risk

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Abstract

In the wild, prey species often live in the vicinity of predators, rendering the ability to assess risk on a moment-to-moment basis crucial to survival. Visual cues are important as they allow prey to assess predator species, size, proximity and behaviour. However, few studies have explicitly examined prey's ability to assess risk based on predator behaviour and orientation. Using mosquitofish, *Gambusia holbrooki*, and their predator, jade perch, *Scortum barcoo*, under controlled conditions, we provide some of the first fine-scale characterisation of how prey adapt their behaviour according to their continuous assessment of risk based on both predator behaviour and angular distance to the predator's mouth. When these predators were inactive and posed less of an immediate threat, prey were often found within the attack cone of the predator showing reductions in speed and acceleration, characteristic of predator-inspection behaviour. However, when predators became active, prey swam faster with greater acceleration and were closer together within the attack cone of predators. Most importantly, this study provides evidence that prey do not adopt a uniform response to the presence of a predator. Instead, we demonstrate that prey are capable of rapidly and dynamically updating their assessment of risk and showing fine-scale adjustments to their behaviour.

Introduction

The threat of predation is ubiquitous for many species. In order to survive, prey must detect and avoid predators, as well as meet daily energy requirements. A problem for prey species arises from the fact that anti-predator behaviours such as increased vigilance (1-3), hiding (4-7) and reduced activity rates (8-10) inherently decrease the amount of time and energy available for important fitness-enhancing behaviours, such as foraging, mating or territorial defence (11). However, individuals are more conspicuous (12) and less vigilant (13-15) while engaged in these important fitness-enhancing behaviours, putting them at greater risk of predation. Due to the opportunity costs that arise from these anti-predator behaviours, prey should ideally adjust the intensity of anti-predator behaviour to the level of risk within their environment, a concept referred to as the risk sensitivity hypothesis (16, 17). Ultimately, this ability to assess and respond appropriately to risk is an important factor determining prey survival.

To assess risk, prey must first detect the presence and location of predators in their environment. Research has shown that prey utilise chemical, visual, auditory and tactile cues to gather information on risk (18-20). Within certain predator-prey systems, visual cues may be particularly important in allowing prey to assess risk based on predator species (21, 22), body size (23), gape size (24), body posture (16) and proximity (25). California ground squirrels (*Spermophilus beecheyi*) and slimy sculpin (*Cottus cognatus*) increase the intensity of their anti-predator responses when confronted with large predators compared to small predators (25, 26). Columbian black-tailed deer (*Odocoileus hemionus columbianus*) increase flight initiation distances when humans approach more directly and at faster speeds (27). Even at close range, some fish use visual cues to avoid the mouth of a predator during inspection behaviour given that the region in front of its mouth (sometimes referred to as the 'attack cone') poses the greatest threat (28, 29). In fact, prey fish use this visual information in an anti-predator behaviour called the fountain effect in which they manoeuvre away from the predator's mouth and towards the blind spot by the tail (30).

These studies underscore the ability of prey to assess the level of risk within their environment and respond in a graded, threat-sensitive manner. Furthermore, they point to the importance of visual cues in mediating prey responses to predators. However, few studies have investigated the ability of prey to continuously assess predation-risk as a function of visual information gleaned from predator behaviour. This question is particularly relevant for prey species living in constant proximity to potential predators, a scenario that is common throughout nature. For instance, Pitcher (31) estimated that free-ranging groups of roach, *Rutilus rutilus*, were seldom more than two meters away from predatory pike, *Esox lucius*, meaning they are constantly within striking distance of a predator. This is similar for many populations of Trinidadian guppies, *Poecilia reticulata*, living in high predation habitats (32). In these scenarios, Pavlov and Kasumyan (33) speculate that maintaining visual contact may be more adaptive than moving away as it allows prey to monitor predator behaviour. Indeed, Magurran and Pitcher (34) found that minnows, *Phoxinus phoxinus*, swimming in the presence of pike predators, *Esox lucius*, shifted between various anti-predator behaviours, escalating the severity of their response as pike shifted from stationary behaviour to stalking or striking behaviour.

The level of threat posed by a predator depends not just on its behaviour, but also on its relative proximity and orientation to the prey. Surprisingly, the extent to which prey integrate these additional variables into their risk assessment is relatively unknown (although see (35)). This apparent gap in the predator-prey research is due in part to the historic lack of advanced

automated tracking software but also to the tendency to treat risk as a fixed factor (36). As a result, little is known about how prey gauge the threat posed by a predator on a moment-to-moment basis or whether they incorporate this information into their behavioural decisions. We sought to investigate how prey adjusted their behaviour in response to predator behaviour and orientation by allowing predator and prey to interact in controlled conditions. We hypothesized that prey would adjust their behaviour based on the predator's activity level and based on where they were located in relation to the predator's mouth. Specifically, we predicted that prey would increase anti-predator behaviours, reflected by increases in swimming speeds, reduced neighbour distances and increases in acceleration (34), when they were in the attack cone in front of the predator, and when the predator was active rather than inactive. Finally, we sought to characterise for the first time the exact shape of the relationship between these response variables and the relative alignment of predator and prey.

Methods:

Collection and Husbandry:

Eastern mosquitofish, *Gambusia holbrooki,* with standard length of 22.5 ± 2.3 mm (mean ± s.d.) were collected from Manly Dam, Balgowlah, Australia (33°46′35.45″S, 151°14′50.38″E), where they would have been subject to predation by various fish species, including silver perch (*Bidyanus bidyanus*), who are from the same family as the predators used in this experiment (jade perch, *Scortum barcoo*). Mosquitofish were collected from Manly Dam in October 2016 and transported to a temperature-controlled aquarium at the University of Sydney. All fish were housed in large stock tanks maintained at 24°C with a 12:12 light:dark cycle and fed fish flake daily. Commercially-bred jade perch with standard length of 91.5 ± 1.6 mm (mean ± s.d.) were housed in individual tanks. Previous work on jade perch found that these predators innately recognize mosquitofish as prey, although prey capture rates are greater in perch with experience of live mosquitofish prey (37). To standardise each predator's foraging experience, all predators were fed a mix of pellets and live mosquitofish daily. All fish were acclimated to lab conditions for a minimum of 2 weeks before experiments began. This work was approved by the University of Sydney Animal Ethics Committee (ref 2016/1077) and was carried out in accordance with local regulations.

Experimental Apparatus and Protocol:

Experimental tanks consisted of two concentric circular arenas placed in a larger square tank with water flow between all compartments (Figure S1). The outer circular wall was opaque and tapered so that it had a diameter of 572 mm at the bottom of the tank and a diameter of 692 mm at the water's surface. Tanks were filled to a depth of 70 mm and kept at the same temperature as the stock tanks. The inner transparent circular arena was used to hold perch during the experiments and had a diameter of 283 mm. A single perch (the predator) was placed in the inner enclosure the night before experiments began and given an additional hour to acclimate in the morning after the lights were turned on. To standardise the olfactory cues in the experimental tank, no predators were fed within 24 hours of trials. After the predator's acclimation period, mixed sex groups of 10 mosquitofish (the prey) were released into the outer annulus of the test tank. After a one-minute acclimation period, trials were filmed for 12 minutes using a Canon G1X camera filming at 1080dpi and 24 fps. A total of 180 mosquitofish were used in 18 separate trials with 18 different perch predators such that all fish were tested only once.

Video Tracking and data extraction:

Videos were formatted and cropped using VirtualDub (v1.9.8) then uploaded to the manual tracking software CTrax (38). Using this automated tracking software, the *x*, *y* coordinates of all fish (both predator and prey) were recorded at each frame over the 12-minute trials. Trajectories were then hand corrected using the Fixerrors GUI in MATLAB so that each fish had an unbroken record of its location throughout all 17,280 frames (see Figure S1).

Using a known ratio of pixels to mm, *x*, *y* coordinates were converted to mm, then used to calculate predator and prey behaviour. Predator coordinates were used to calculate instantaneous speed and turning speed. To account for spurious fluctuations in tracked movement, coordinates were smoothed using a rolling average that spanned 5 frames (208ms). Using the same 5 frame smoothing window, prey coordinates were used to measure median swimming speed (mm/s), median nearest neighbour distances (mm) and median acceleration (mm/s^2) for each individual prey. We calculated median swimming speeds and acceleration because both behavioural measures are highly responsive to context (39).

Similarly, we used nearest neighbour distances as a measure of risk-perception given that prey often form more compact and cohesive groups in response to increased risk (40).

Perch behaviour was characterized by periods of activity, marked by high speeds and high turning speeds, and periods of inactivity, marked by low speeds and low turning speeds. This was determined after histograms of predators' instantaneous speed and turning speed revealed bimodal behavioural states (Figure S2). Using these instantaneous speed and turning speed thresholds, predator behaviour could be categorised into "active" or "inactive" states (see Supplemental methods). As perch typically stalk prey before striking, the probability of the predator striking at prey increases when they become active (37). Therefore, we analysed prey behaviour based on predator activity state.

Previous experiments have also demonstrated that prey behave differently when in front of a predator and tend to avoid the 'attack cone' region immediately in front of the predator's mouth (29, 41). In light of this work, we analysed prey behaviour based on their position relative to the predator's mouth. To do this, we created a series of 5º bins radiating out from in front of the predator's snout (0º to 5º) to directly behind the predator (175º to 180º). We then calculated the behaviour of each individual prey (median speed, acceleration and nearest neighbour distance (NND)) in each 5º bin based on whether the predator was active or inactive.

Individual prey behaviour was only recorded within a 5º bin if the individual remained within the bin for at least 5 frames. We did not investigate lateralised behaviours in either the predator or prey and instead averaged prey behaviour across the predators' left and right sides. To avoid any effect of tank geometry on prey behaviour, we analysed prey within two predator body lengths of the predator (average predator standard length: 91.5 ± 1.6 mm, therefore prey behaviour was limited to within 183mm of the predator's centre of mass).Once all filtering had been applied, there was an average of 163 individual prey measures within each bin (range: 147 - 176 individuals), which was derived from an average of 71 timesteps (range: 5 - 1839 frames).

Statistical Analysis:
Each measure of prey behaviour was tested in mixed effect models against the interaction between predator state and angle to the predator's mouth. To fully capture the fine-scale adjustments in prey behaviour, which were often non-linear, we included orthogonal 1st, 2nd, and 3rd order polynomials to investigate whether the quadratic term significantly improved the regression compared to the linear term or the cubic term significantly improved the regression compared to the quadratic term. Orthogonal polynomials, using the poly() function in R, were used to reduce multicollinearity and improve model stability (42). While the linear fit was often significant, it failed to capture the essence of these behavioural responses (see below). When there was a significant interaction between predator state and angle, prey behaviour was tested against angle and the orthogonal polynomials of angle separately based on whether predators were active or inactive. Depending on which degree polynomial was significant within the main model, the subsequent subsetted model included the same degree polynomial along with all lower degree polynomials.

Within each mixed effect model, which we created using the lme function in R (43), prey identity was nested within group and included as a random effect. This was done to account for the non-independence of individuals within the same trial. To meet the assumption of homogeneity of variance, response variables were transformed using the ordered quantile

(ORQ) normalization transformation (44), though graphs were produced using raw data to increase interpretability.

To visualise how prey adapted their movements in response to predator activity state and location, heat plots of prey direction of movement and speed in relation to the predator's position and orientation were created. To do this, we calculated the mean velocity of all prey movements that occurred in each cell of a 17 mm x 17 mm gridded array, centred with the predators positioned at (0,0) and facing along the positive y-axis. Within each cell of this array, we also calculated the mean orientation of prey in relation to the predator. This bin size was selected because it represents the standard length of the smallest mosquitofish used within any trial (17.32 mm). This was done separately for times when predators were active and inactive.

Given the correlational nature of our analysis, it is possible that our results are bidirectional. That is, predators may shift activity and position in response to prey, or prey may shift behaviour in response to predator activity and angular position. In this case, we feel the latter interpretation is more likely given the spatial dispersion of prey throughout the arena rendering the ability of predators to respond in a uniform way to individual or grouped prey difficult. With prey dispersed around the arena, predators would have encountered the same value of prey behaviour (speed, NND and acceleration) at multiple angular positions at any one time.

Results

Predators shifted between active and inactive activity states (Fig. S3), spending an average of 58% of each trial inactive and 42% active. Prey adjusted their median swimming speed as a function of the interaction between predator activity state and angular position relative to the predator's mouth (i.e. State*Angle^3; see Table 1). In particular, prey showed a greater range of speeds across angular positions when predators were inactive and generally moved more slowly as they approached the head or tail of the predator (Table S1) (Fig. 1 and see vector length (represented by the arrows) in Fig. 2). The reductions in speed when in front of a predator potentially allow individuals to update information about risk in a manner akin to predator inspection behaviour (45, 46). While prey slowed down in front of inactive predators, swimming speeds were not reduced to the same extent when in front of active predators (Fig. 1). This is likely due to the greater risk associated with occupying positions within the attack cone and can help explain the pronounced flow of prey away from the predator's mouth and towards its tail during periods of activity in Fig. 2.

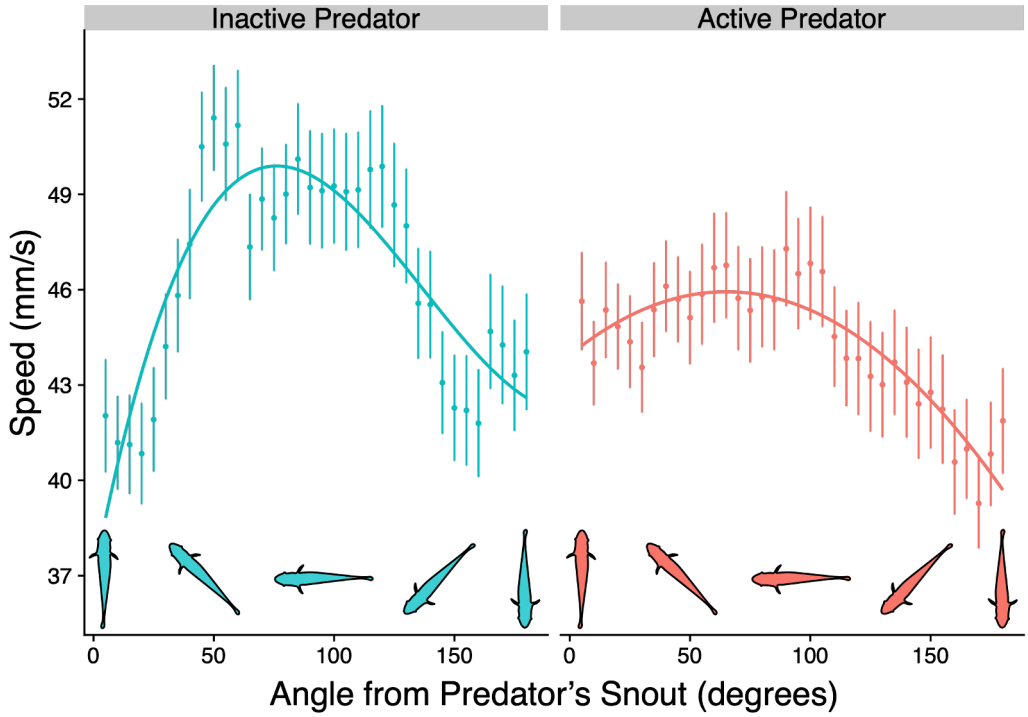

Figure 1: Graph of median prey swimming speed (mm/s) against angle from predator's snout when predators were inactive (blue) and active (red). There was a significant cubic relationship when predators were inactive and significant quadratic relationship when predators were active (Table S1). Mean median speeds and standard errors are shown.

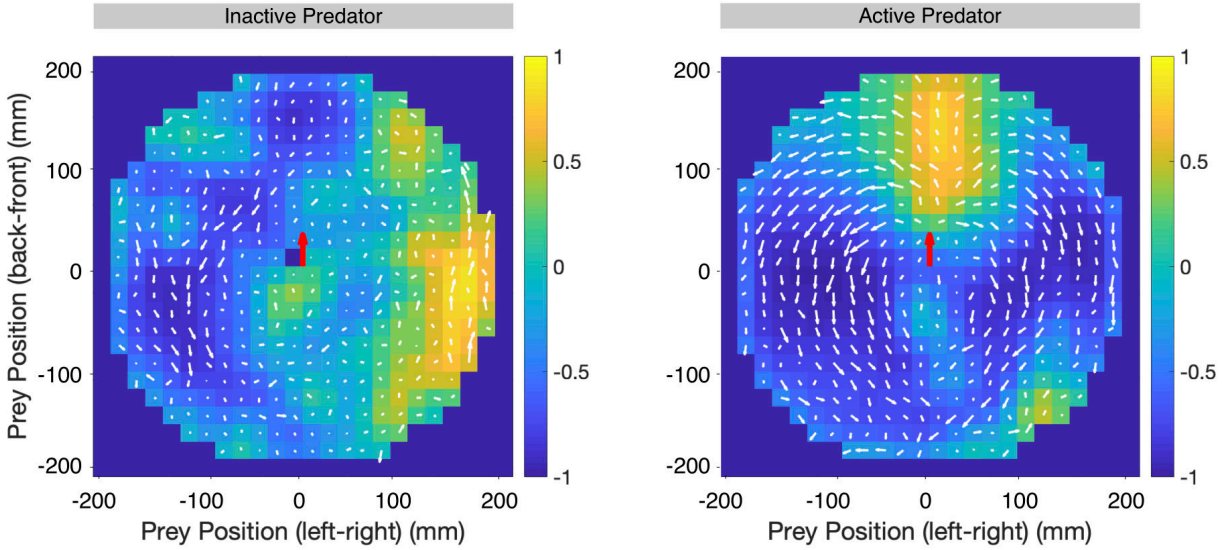

Figure 2: Heat map of mean prey direction of movement and speed (as shown by the vector field (white arrows)) in relation to the predator (depicted in red at the origin of the plot). Warmer colours indicate when prey move in the same direction as the predator, cooler colours indicate when predator and prey direction of movement are opposed (measured as the cosine of the angle between the prey and predator headings).

Along with these shifts in median speeds, prey also adapted their median distances to nearest neighbours as a function of the interaction between predator state and angular position relative to the predator's mouth (Table 1). Generally, prey swam closer together in front and behind the predator, although the shape of this relationship changed with predator state (Table S1). When predators were inactive, NND was lowest when prey were behind the predator whereas when predators were active, NND was lowest in front of the predator (Fig. 3). While grouping more closely is a common response to situations of heightened risk (47), our results demonstrate an ability to adjust nearest neighbour distances in response not only to the presence of the predators, but also to slight changes in predator behaviour and orientation.

Prey also showed a shift in median acceleration based on predator state and angular position relative to the predator's mouth (Table 1). Given that rapid acceleration, potentially resulting from fast start escape behaviour (48), is an energetically taxing behaviour, prey should ideally employ this behaviour in extreme situations, such as when they find themselves in front of an active predator. Accordingly, we found a significant relationship between acceleration and angular position when predators were active with the fastest accelerations occurring directly in front of the predator's mouth and declining as they neared the predator's tail (Table S1). When predators were inactive, there was a significant quadratic relationship with prey showing slightly greater acceleration when located to the side of the predator (Fig 4).

When the predators were inactive, prey fish tended to swim anti-clockwise around the annulus, with no discernible directional coordination with respect to the predator's orientation (Fig. 2). However, once predators became active, prey fish fanned away from the predator's snout and towards the predator's tail, a pattern termed the fountain effect in the routine behavioural decisions of prey (30).

Table 1: Results from individual mixed effect models tested against each measure of prey behaviour. Individual nested within trial was included in each model as a random effect.

				Conf. Int.			
		Value	Std. Error	Lower	Upper	t-value	p-value
Median Speed (mm/s)	(Intercept)	0.01	0.06	-0.10	0.12	0.15	0.88
	State	-0.06	0.01	-0.08	-0.03	-4.32	< 0.001
	Angle	-1.52	0.95	-3.38	0.35	-1.60	0.11
	$Angle^2$	-14.64	0.96	-16.52	-12.77	-15.30	< 0.001
	$Angle^3$	5.23	0.96	3.36	7.10	5.47	< 0.001
	State*Angle	-5.54	1.36	-8.21	-2.87	-4.06	< 0.001
	State*$Angle^2$	10.94	1.36	8.27	13.61	8.02	< 0.001
	State*$Angle^3$	-5.01	1.36	-7.68	-2.35	-3.69	< 0.001
Median Nearest Neighbour Distances (mm)	(Intercept)	0.00	0.04	-0.07	0.08	0.03	0.97
	State	0.00	0.02	-0.03	0.03	-0.04	0.96
	Angle	-7.71	1.22	-10.09	-5.33	-6.34	< 0.001
	$Angle^2$	-3.65	1.22	-6.05	-1.25	-2.98	< 0.001
	$Angle^3$	6.64	1.22	4.25	9.04	5.43	< 0.001
	State*Angle	12.61	1.74	9.19	16.03	7.23	< 0.001
	State*$Angle^2$	-1.99	1.74	-5.41	1.42	-1.14	0.25
	State*$Angle^3$	-7.05	1.74	-10.46	-3.64	-4.05	< 0.001
Median Acceleration (mm/s^2)	(Intercept)	-0.05	0.06	-0.16	0.06	-0.82	0.41
	State	0.06	0.01	0.04	0.08	4.79	< 0.001
	Angle	-0.26	0.93	-2.09	1.57	-0.28	0.78
	$Angle^2$	-2.19	0.94	-4.03	-0.35	-2.33	0.02
	$Angle^3$	1.20	0.94	-0.64	3.04	1.28	0.20
	State*Angle	-9.83	1.34	-12.46	-7.21	-7.35	< 0.001
	State*$Angle^2$	4.08	1.34	1.46	6.70	3.05	< 0.003
	State*$Angle^3$	0.37	1.33	-2.25	2.98	0.28	0.78

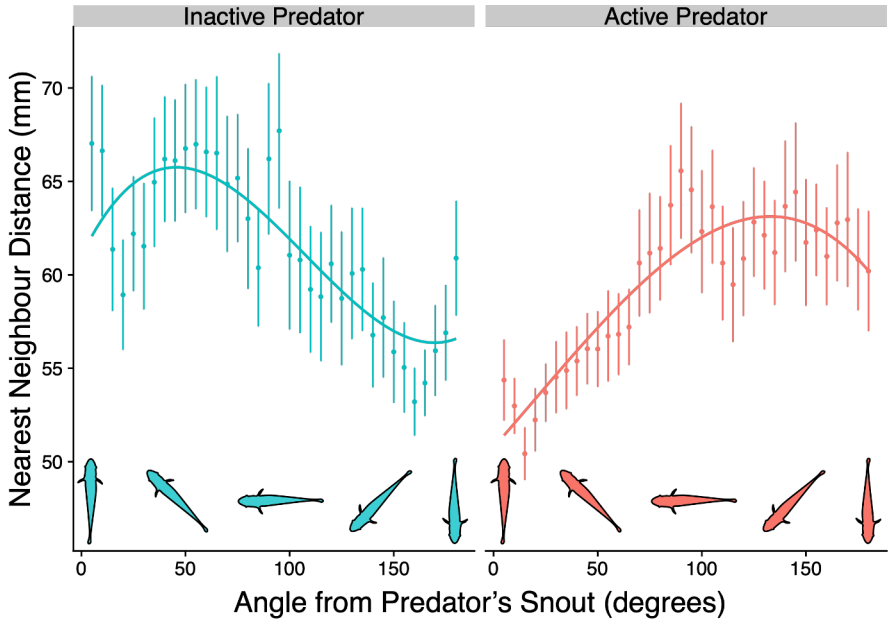

Figure 3: Graph of median nearest neighbour distances (mm) against angle from predator's snout when predators were inactive (blue) and active (red). There was a significant cubic relationship between angular position and NND when predators were inactive and significant quadratic relationship when predators were active (Table S1). Mean neighbour distances and standard errors are shown.

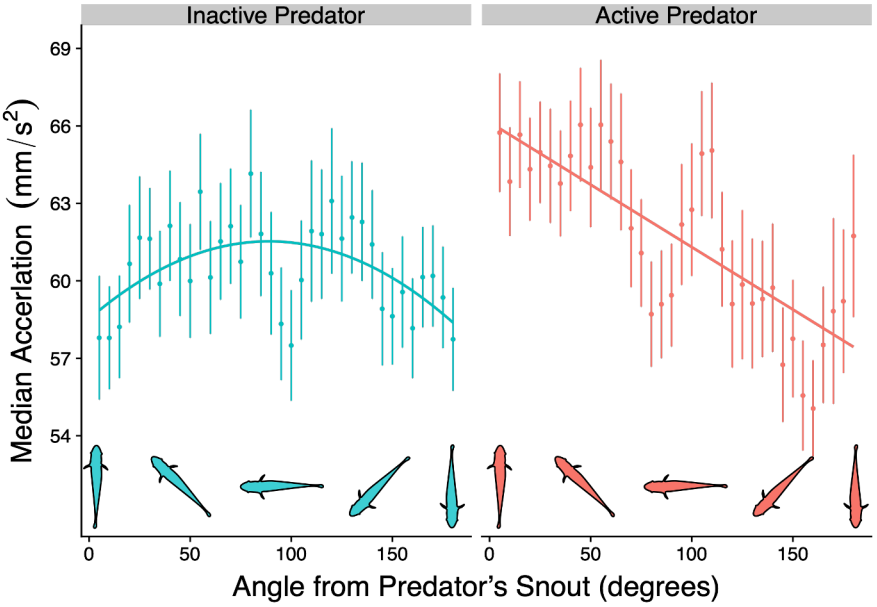

Figure 4: Graph of median acceleration (mm/s^2) against angle from predator's snout when predators were inactive (blue) and active (red). There was a significant quadratic relationship between acceleration and angle when predators were inactive and active (Table S1). Mean acceleration and standard errors are shown.

Discussion

Here we provide evidence that prey continuously update their risk assessment and adjust their behaviour based on predator behaviour and their position relative to the predator's mouth. When predators were inactive and posed less of an immediate threat, prey showed pronounced inspection behaviour within the attack cone of the predator with reductions in speed and acceleration. However, when predators began to move and therefore posed a greater threat, prey swam faster, closer together and increased acceleration within the attack cone of predators. Generally, during periods of reduced risk when predators were inactive, prey swam in circles around the annulus. When predators were active, prey adapted their behaviour by fanning away from the predator's mouth and towards its tail, a manoeuvre referred to as the fountain effect (30).

In the wild, prey species often live in the vicinity of predators, rendering the ability to assess risk on a moment-to-moment basis crucial to survival. Seemingly maladaptive behaviours, such as approaching and inspecting potential sources of risk, may therefore allow prey to gain information regarding risk (49, 50). Previous work has shown that prey utilize visual cues such as eye width and gape size to assess the level of threat (24, 51), indicating that inspection of the most dangerous region by a predator's head can provide vital information. In the current study, we found that when predators were inactive, prey approached regions in front of the predator's mouth at slower speeds. While counter intuitive, this speed reduction may decrease prey conspicuousness (52, 53) while enhancing visual acuity through reduced motion blur (54) and improved flow detection through the lateral line. These mechanisms might therefore increase the likelihood of detecting predatory attacks when in risky locations (55, 56). In accordance with the risk sensitivity hypothesis, we found that once predators were active, prey increased swimming speeds within the attack cone of the predator and swam away from its head and towards the relative safety of its tail. These increased speeds may reflect the immediate need to get out of striking distance of the predator and leave the 'attack cone' directly in front of its mouth (28, 29, 41, 57, 58). In this way, prey appear to employ adaptive information gathering behaviours during times of lower risk and shift to safer, more evasive behaviours as predators posed a greater threat.

In tandem with this shift to faster swimming in front of predators, prey reduced distances between themselves and their nearest neighbours when predators were active. Grouping more closely is a common evolutionary response to predation (59-62). Indeed, research suggests that individuals within a group can reduce risk by moving towards neighbours and by positioning themselves closer to the centre of the group, ultimately resulting in the formation of denser aggregations (47, 63). This can explain why in many systems, we see the formation of more compact groups after exposure to a predator (39, 64-67). In the current study, we found the smallest neighbour distances occurred when prey were directly in front of an active predator, suggesting that prey were capable of gauging risk not based solely on predator presence, but based on the predator's behavioural state and angular position. The fact that prey did not consistently form more cohesive groups in the presence of a predator implies that there may be costs associated with remaining cohesive. These costs, for example, could include increased cognitive demands associated with the coordination of this behaviour, or increased competition for resources. Ultimately, understanding how animal decision making circuits integrate multiple forms of information including the state and position of the predator, the position of neighbours and the costs and benefits of cohesion, will provide an intriguing avenue for future research, particularly from a neurological perspective.

When predators became active, prey switched between swimming around the annulus to a manoeuvre commonly described as the 'fountain effect' (30), in which prey fan away from the predator's mouth and towards the blind spot by its tail. Traditionally, observations of this behaviour describe prey rapidly accelerating out of the predator's attack cone in response to a direct strike (34, 68). While these flash fountain manoeuvres in direct response to predator strikes are visually apparent, it is interesting to note that the fountain pattern in this study emerged by averaging prey behaviour over the course of a trial, suggesting that these movement patterns around a predator may be occurring more passively through slight adjustments to routine behaviour. This manoeuvre may act as a way for prey to increase survival by avoiding the dangerous area in front of a predator while maintaining cohesion by reforming groups behind the threat, as reflected in the decreasing nearest neighbour distances found towards the tail of the predator. Our findings represent the first description of the fountain manoeuvre in averaged prey behaviour and ultimately serve to underscore prey's ability to integrate information about the risk posed by different predator behaviours and different regions of the predator, lending further support to the risk sensitivity hypothesis.

By using basic routine behavioural adjustments based on predator activity and their position relative to a threat, prey fish may be able to minimise their exposure to risk through energetically efficient means. However, when prey inevitably find themselves in a dangerous situation (or position), they may need to employ more energy-consuming anti-predator responses, such as fast starts. Fast starts, or c-starts, are marked by sudden bursts of acceleration away from a threatening stimulus (48). In the current study, we found that acceleration was greatest when prey were directly in front of an active predator and decreased almost linearly with distance from the predator's mouth. Previous research has shown that the ability to rapidly put distance between yourself and danger is a highly adaptive and conserved behavioural mechanism (69). Evidence for the advantages of fast start behaviours have been found in research using largemouth bass and four different prey species. In that study, predators were increasingly likely to abort an attack as prey acceleration increased (70). Similarly, the evasion success of prey corresponded to their acceleration rates (71). This means that the ability to preserve energy when risk is low and engage in the most taxing evasive behaviours only when risk is high could be important to the survival of prey species. Fittingly, prey in this study showed the greatest acceleration when in the most extreme situations, namely when they found themselves in the direct path or within striking distance of an active predator.

While previous research has expanded our understanding of how prey behaviour changes as a function of prey hunger levels (72), prey group size (73, 74), prey provenance (75), predator diet (76-78) and predator morphology (24, 79), much of this work has been done through the use of model predators (79), computer animated predators (80), short exposure times (81) or the use of isolated cues, such as conspecific alarm cue (73), heterospecific alarm cue (82) or predator odours (74, 76). Despite the importance of these manipulative laboratory experiments, there is a dearth of empirical studies investigating the importance of predator behaviour in shaping prey behaviour. Many of these previous approaches have reduced predators from interactive agents to "abstract sources of risk" (36), which prevents researchers from detecting some of the more nuanced ways in which prey can respond to the presence of a predator. We found that prey reduce risk by continuously adjusting their routine behaviour based on different information gleaned from visual cues. We found that prey respond continuously to predator activity levels and adjust behaviour based on angular distance from the predator's mouth, demonstrating an ability to assess risk on a moment-to-moment basis and adjust behaviour accordingly. It is worth noting that while we discuss our

results from the perspective of the prey, we did not consider how predators changed their behaviour as a function of prey behaviour. Ultimately, understanding predator induced changes in prey behaviour and prey induced changes in predator behaviour will provide important insight into the behavioural arms races within these predator-prey systems.

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Supplementary methods:

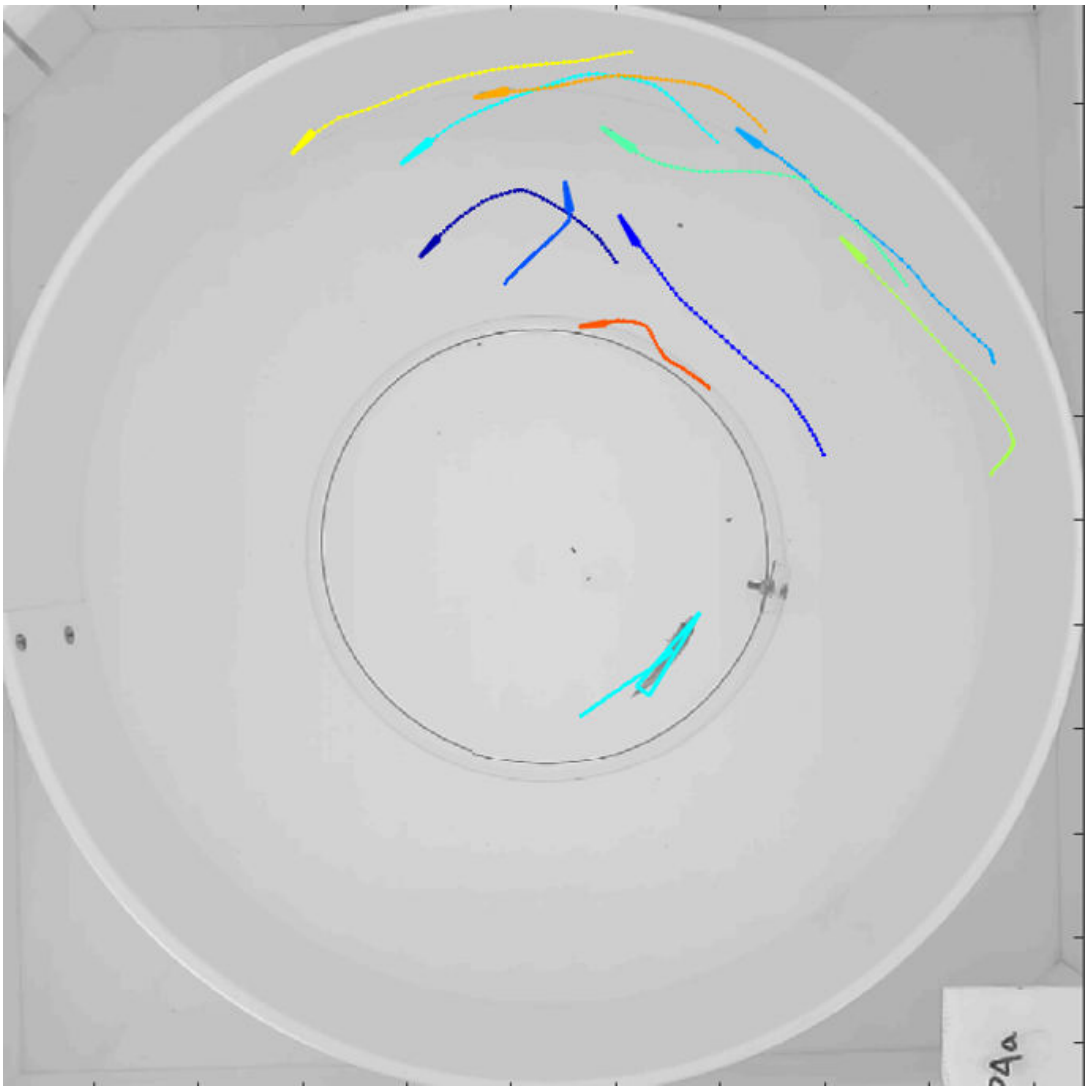

Figure S1: Example of experimental setup and video tracking from predator 4 trial.

Table S1: Results from mixed effect models against each measure of prey behaviour when predator state is considered separately. Individual nested within trial was included in each model as a random effect.

	Predator State	Fixed Effects	Value	Std. Error	Conf. Int. Lower	Conf. Int. Upper	t-value	p-value
Median Speed (mm)	Inactive	Intercept	0.00	0.06	-0.11	0.12	0.08	0.94
		Angle	-1.31	0.67	-2.63	0.01	-1.94	0.05
		$Angle^2$	-10.51	0.68	-11.84	-9.19	-15.53	< 0.001
		$Angle^3$	**3.96**	**0.67**	**2.64**	**5.27**	**5.90**	**< 0.001**
	Active	Intercept	-0.02	0.06	-0.13	0.09	-0.32	0.75
		Angle	-4.42	0.64	-5.68	-3.16	-6.88	< 0.001
		$Angle^2$	**-2.98**	**0.64**	**-4.23**	**-1.73**	**-4.66**	**< 0.001**
		$Angle^3$	-0.06	0.64	-1.31	1.19	-0.09	0.93
Median NND (mm)	Inactive	Intercept	0.01	0.05	-0.08	0.10	0.24	0.81
		Angle	-5.70	0.84	-7.35	-4.05	-6.77	< 0.001
		$Angle^2$	-2.56	0.85	-4.22	-0.90	-3.02	0.00
		$Angle^3$	**4.85**	**0.84**	**3.21**	**6.50**	**5.78**	**< 0.001**
	Active	Intercept	0.00	0.04	-0.09	0.08	-0.09	0.93
		Angle	3.44	0.80	1.88	5.01	4.31	0.00
		$Angle^2$	**-4.10**	**0.80**	**-5.66**	**-2.54**	**-5.15**	**0.00**
		$Angle^3$	-0.43	0.79	-1.98	1.13	-0.54	0.59
Median Acceleration (mm/s^2)	Inactive	Intercept	-0.05	0.06	-0.16	0.07	-0.78	0.44
		Angle	-0.50	0.66	-1.78	0.79	-0.75	0.45
		$Angle^2$	**-1.60**	**0.66**	**-2.89**	**-0.30**	**-2.42**	**0.02**
	Active	Intercept	0.04	0.06	-0.07	0.15	0.70	0.48
		Angle	**-7.53**	**0.65**	**-8.79**	**-6.26**	**-11.66**	**0.00**
		$Angle^2$	1.07	0.64	-0.19	2.33	1.67	0.09

Trajectory Analysis:
Both predator and prey coordinates were smoothed using a moving average spanning 208ms (5 frames of video) and converted into real-world coordinates using a known reference length within the videos.

Identifying Predator States:
Histograms of both the predators' instantaneous speeds (Fig. S2a) and turning speeds (Fig.S2b) were bimodal, indicating the presence of two behavioural states. Plotting predators' instantaneous speeds versus their instantaneous turning speeds revealed more detail of these states (Fig. S2c). One state was associated with higher speeds and turning speeds (state 1), which we call the 'active state'. The other was associated with relatively lower speeds and turning speeds (state 2), which we call the 'inactive state'. We take the projection of a predator's speed and turning speed along the line joining the centroids of the active and inactive state (denoted by an arrow in Fig. S2c). We define the halfway point between the two to be the boundary between these two states (as shown by the segment halfway along the arrow), and determined the occasions when each predator was in the 'active state – state 1' (top right region of the Fig 2c) or an 'inactive state – state 0' (bottom left region of Fig. S2c). Because measurements of instantaneous speed and turning speed were noisy, we attempted to identify more contiguous periods when a predator was in the active state. This was done by forcing small periods of inactivity of less than 2 seconds which are found between active periods, to also be marked as active. Results are detailed in Figure S3.

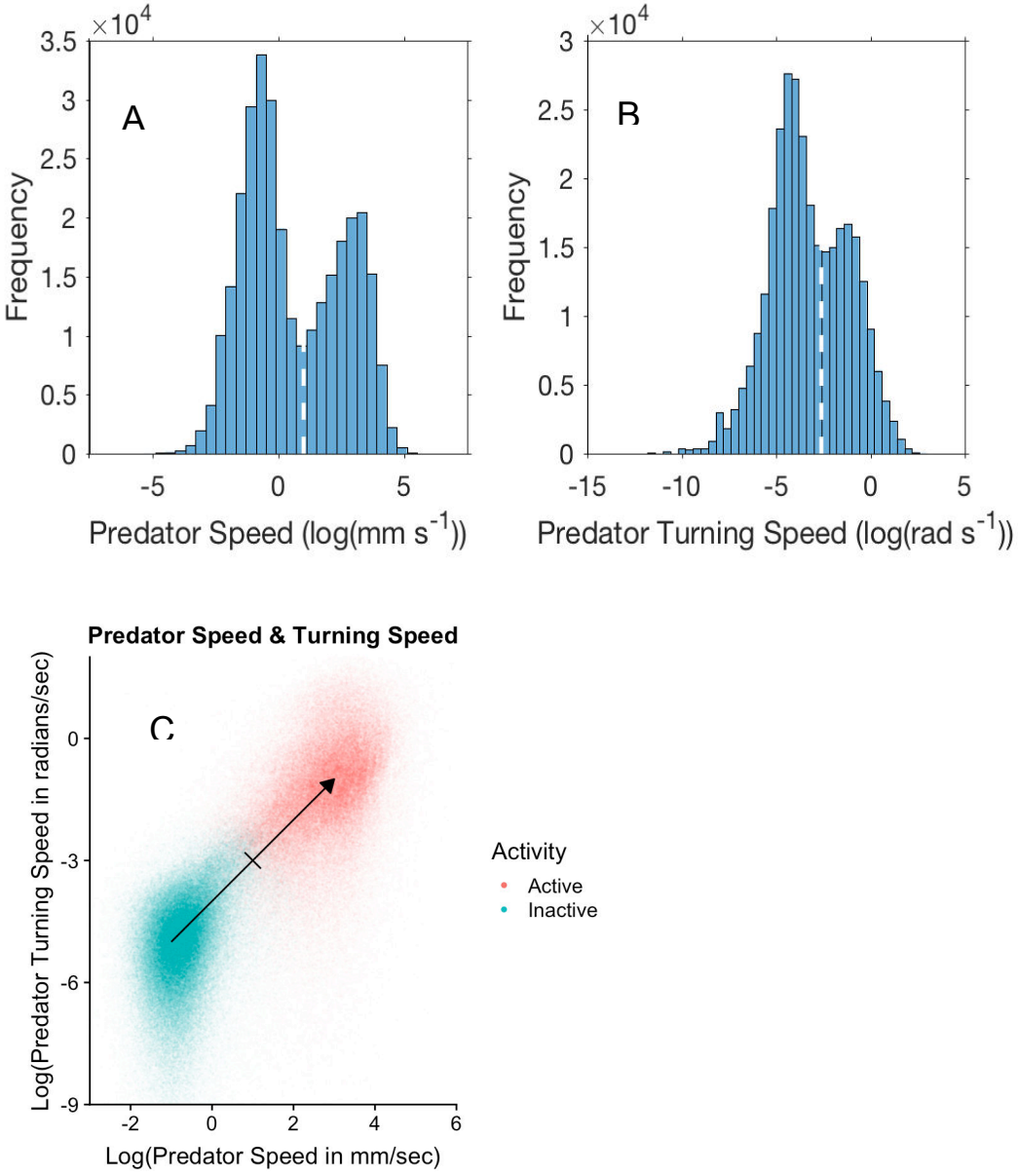

Figure S2: Frequency histograms of (a) log predator speed and (b) log predator turning speed. (c) Log turning speed versus log speed for all predators. We use the projection of a predator's instantaneous speed and turning speed onto the arrow in in (c) to label the predator as 'active' (red, top right) or 'inactive' (blue, bottom left) at a given point in time.

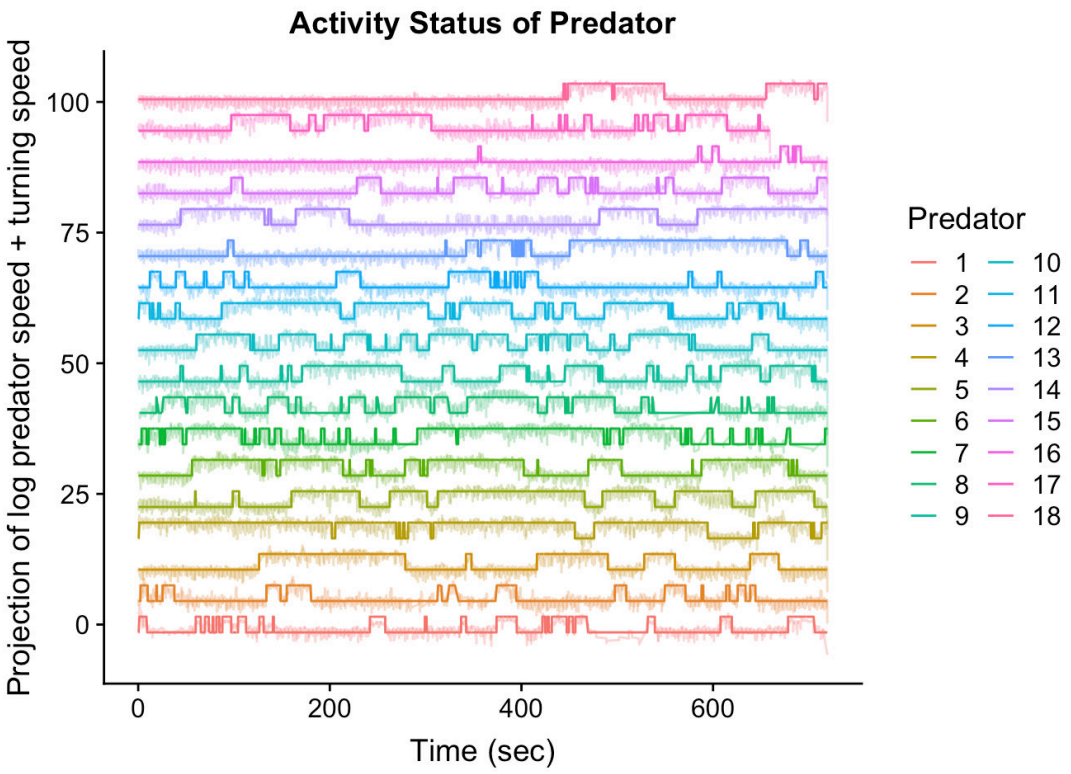

Figure S3: Labels of time periods of activity and inactivity for each of the 18 predator fish. The projection of a predator's speed and turning speed along the line joining the centroids of the active and inactive state (denoted by an arrow in Fig. S1c) is shown as the noisier, faint signal on each line. The solid, binary indicator of 'active' vs. 'inactive' state for each predator is shown on top (after filtering). Each predator's line is offset vertically from the previous one so that they are all visible.